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A new Middle Ordovician bivalve–siliceous sponge–microbe reef-building consortium from North China

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ABSTRACT

A new reef-building consortium from a Middle Ordovician succession of the western North China Platform is described, consisting mainly of bivalves, siliceous sponges, and microbial carbonates (*Epiphyton*-like, *Renalcis*-like and *Girvanella* calcified microbes, and microcrystalline microstromatolites), in addition to minor brachiopods, *Amsassia* and *Rhabdotetradium*. The bivalves are thin-walled and mostly articulated, indicating in situ preservation. The siliceous sponges are characterized by regularly spaced spicule networks embedded within micrite, which partly grade into peloidal textures. Three main types of bivalve–sponge associations are found: (1) larger bivalves (2–13 mm) encrusted by sponges, (2) sponges occupying internal spaces of larger bivalves, and (3) smaller (0.2–0.4 mm) bivalves embedded within sponge spicule networks. Microbial carbonates either cover the upper surfaces of siliceous sponges and bivalves, or occur independently as centimeter-scale patches. The reefal boundstones were constructed mainly by bivalves, siliceous sponges and microbes, which were subsequently encrusted and stabilized by additional sponges and microbes. Extensive early marine cementation forming fibrous cement helped stabilize the reef framework. The co-occurrence of bivalves and siliceous sponges is possibly analogous to modern-day counterparts in which sponges encrust bivalves or bivalves are living within sponges, suggesting a symbiotic relationship. The bivalve–siliceous sponge–microbial reefs of this study, together with other Ordovician reefs, represent the changeover from microbial- to skeletal-dominated reefs during the Middle Ordovician. The current example may represent an ancestral association of bivalve–siliceous sponge–microbe reefs, similar to those in the Mesozoic and Cenozoic, thus shedding light on the roots of such associations.

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1. Introduction

Skeletal reef-builders such as stromatoporoids, corals, bryozoans, and calcareous algae began to dominate reefs during the Middle–Late Ordovician, which was the first time interval of the Phanerozoic exclusively colonized by skeletal-dominated reefs (e.g., Alberstadt et al., 1974; Kapp, 1975; Desrochers and James, 1989; Webby, 2002; Li et al., 2004; Adachi et al., 2009, 2012). Although the faunal components of these Middle–Late Ordovician reefs were generally considered to have persisted until the Late Devonian mass extinction (Wood, 1999), several characteristic reef-building associations are also known to be confined to the Ordovician (e.g., those involving *Amsassia* and tetradiids),

possibly reflecting the early diversification of reef-building organisms (Webby, 2002; Kwon et al., 2012; Lee et al., 2014b). An understanding of Ordovician skeletal-dominated reefs would therefore help determine the early evolutionary history of skeletal reefs, which flourished throughout the rest of the Phanerozoic.

The North China Platform, a mixed carbonate–siliciclastic platform developed on the Sino-Korean Block during the Cambro-Ordovician, yields a variety of early Paleozoic reefs (Webby, 2002; Wang et al., 2012; Choh et al., 2013; Lee et al., 2016). However, a detailed study of the early Paleozoic reefs has yet to be performed, although some recent studies have indicated that the platform contains important information regarding the early evolution of skeletal reef-builders (e.g., Lee et al., 2014b). In this study, we report on a new bivalve–siliceous sponge–microbe reef-building consortium from the Middle Ordovician of the western North China Platform. An understanding of this unique Ordovician reef-building consortium, consisting primarily of bivalves

and siliceous sponges, may improve and expand our understanding of Ordovician reef systems.

2. Geological setting and methods

During the Cambrian and Ordovician, a thick shallow-marine succession (~1800 m thick) developed on the Sino-Korean Block, forming the North China Platform (Meng et al., 1997). The block is now demarcated by major fault and suture zones on its northern, eastern, and southern margins (the Hinggan Fold Belt, Tanlu Fault, and Qinling–Dabieshan Belt, respectively); however, its western margin retains thick platform-margin and deep-basin sediments (Chough et al., 2000). The Ordos Basin (area of ~250,000 km^2), located in the western part of the block, extends across Shaanxi, Shanxi, Gansu, Ningxia, and Inner Mongolia in China (Yang et al., 2008) (Fig. 1A). A thick Ordovician carbonate platform succession containing various reefs occurs in the southern part of the Ordos Basin (Ye et al., 1995; Webby, 2002; Wang et al., 2012; Lee et al., 2014b). The entire Cambro-Ordovician succession of North China is unconformably overlain by Carboniferous sedimentary rocks (Chough et al., 2000; Zhen et al., 2016).

The bivalve–siliceous sponge–microbial reefs of this study were recognized in a quarry outcrop in Chenluzhen County, Tongchuan, Shaanxi Province, China (Fig. 1B). The outcrop, which reveals an ~40-m-thick carbonate succession belonging to the Pingliang Formation (Middle Ordovician) (Ye et al., 1995) that is unconformably overlain by Carboniferous succession (Fig. 2A), consists mainly of massive limestone intercalated with grainstone. The study is based on ~30 specimens of bivalve–siliceous sponge–microbial boundstone from the Pingliang Formation. Microscale structures within the boundstone were observed in ~200 large-format (7.6 × 5.2 cm) thin sections.

3. Results

Several exposures of reefal boundstones are present in a ~20-m-thick interval (Fig. 2A), characterized by extensive occurrences of bivalves with geopetal structures, which are embedded within dark-gray fine-grained limestone (Fig. 2B). The boundstones most likely formed decimeter- to meter-scale structures, although their outlines are obscured, and macro- and mega-scale structures are therefore difficult to discern.

3.1. Thin section analyses

Bivalves, siliceous sponges, and microbialites are the dominant constituents of the Chenluzhen reefs, together with minor brachiopods and the coralomorphs *Amsassia* and *Rhabdotetradium*. Calcite cements commonly co-occur with these biotic components, and occupy ~30% to >90% of the reefs (Fig. 3). Many of the cements are fibrous, with fibers 250–500 μm long and 10–30 μm wide. At least two (and possibly

more than four) stages of fibrous cement growth are present, followed by stage of blocky cement (Fig. 4A).

Bivalves are characterized by two symmetrical articulated shells, which are either very thin (10–20 μm thick) or not preserved (Fig. 4). Two types of bivalves are recognized on the basis of their size. The larger bivalves are 2–13 mm long (Fig. 4A–C), whereas the smaller bivalves are 0.2–0.4 mm long (Fig. 4D). Fibrous cements oriented normal to the substrate commonly occur inside and/or outside the shells of the large bivalves (Fig. 4). The orientations of the bivalves vary, but many are aligned in subhorizontal to subvertical directions (Fig. 3).

Siliceous sponges are characterized by networks of regularly spaced "spicules" embedded within micrite (cf. Hong et al., 2012; Kwon et al., 2012; Hong et al., 2014; Lee et al., 2014a) (Fig. 5). The spicules are 50–700 μm long and 25–65 μm in diameter; they are partly curved in shape and commonly bifurcate or trifurcate. The angles between the spicule rays vary from ~30° to 170°, but only occasionally meet at ~90°. The spicule networks are mostly irregular in outline, and are often accompanied by irregular voids filled with fibrous cements within the networks (Fig. 5A–C, E). Sponge spicule networks are commonly degraded, forming peloidal fabrics (Figs. 4C and 5B, F). A recent study suggests that similar sponge networks from Devonian and Triassic successions may be remains of "keratose" demosponges consisting of skeletal fibers instead of spicules (Luo and Reitner, 2014). Further studies are required to clarify the nature of these enigmatic sponges.

Bivalves and siliceous sponges commonly occur together, but some of the large bivalves are surrounded only by cement without sponges (Fig. 3). The bivalve–siliceous sponge association can be divided into three major types. (1) Siliceous sponges attached to the outer surfaces of large bivalve shells (Fig. 5A–C); in such cases, spicules are commonly aligned parallel to the bivalve shells (Fig. 5B, D). (2) Siliceous sponges occupying the internal space of both large and small bivalve shells (Figs. 4C and 5). (3) Small bivalves embedded in sponge spicule networks (Figs. 4D and 5D). These three types commonly occur together. For example, sponges attached to a large bivalve shell may also incorporate small bivalve shells at the same time (Fig. 5A). Some sponge spicule networks surrounding large bivalves extend to the interiors of bivalves (Fig. 5B).

Microbial carbonates are characterized by calcified microbes, peloids, and microcrystalline microstromatolites (Fig. 6). Calcified microbes consist of bush-shaped branching *Epiphyton*-like microbes and laterally elongate tubular *Girvanella*. *Epiphyton*-like calcified microbes commonly co-occur with, and laterally grade into, peloids, and some encrust the tops of sponges or bivalve shells (Fig. 6A, B). *Girvanella* is often associated with peloids, forming irregular fabrics (Fig. 6C). Chambered calcified *Renalcis*-like microbes rarely encrust bivalve shells (Fig. 6D). Calcified microbes and peloids are commonly covered by convex-upward finely laminated microstromatolites (Fig. 6B). These microstromatolites are composed of alternating microspar and micrite
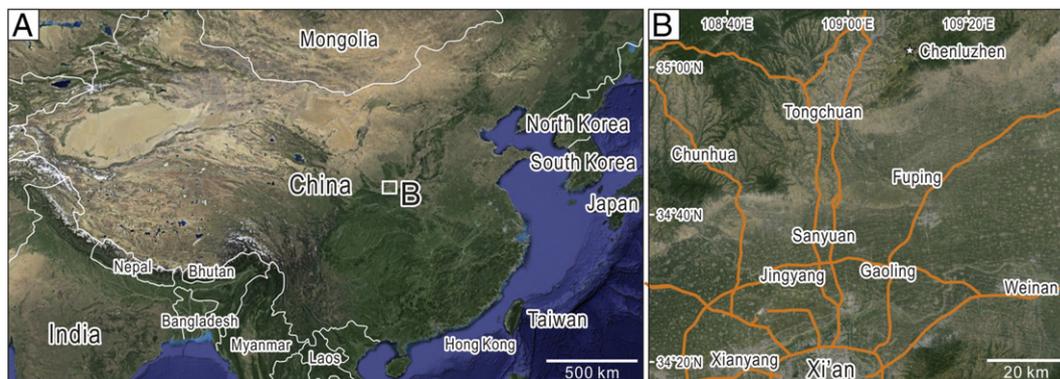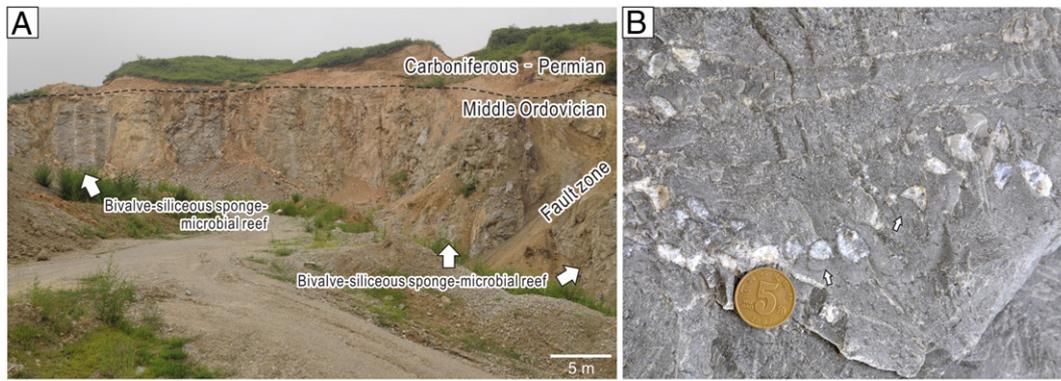

Fig. 1. (A) Satellite image of East Asia, showing the study area marked by a white rectangle. (B) Satellite image of the study area in Shaanxi Province, China. The studied section (Chenluzhen section; 35°02′09″N, 109°10′15″E) is marked by a star.

Fig. 2. (A) Outcrop photograph of the Chenluzhen section. The bivalve–sponge–microbial reefs were identified at three spots in the quarry, marked by arrows. (B) Bivalve–sponge–microbial reef exposed in the outcrop. Recrystallized bivalves can be easily identified from the outcrop, whereas the other reef constituents are not readily identifiable. Note the occurrence of geopetal structures (arrows). Coin for scale is 2 cm in diameter.

layers, and they show no evidence of calcified microbes within them. The remaining microbial carbonates consist of peloids of irregular shape. These peloids co-occur mainly with either calcified microbes or siliceous sponges, and it is not easy to differentiate their origin. The calcified microbes occur mainly as centimeter-scale patches surrounded by calcite cement.

Brachiopods, *Amsassia* and *Rhabdotetradium* occupy minor portions of the reefs (Fig. 7). The brachiopods locally co-occur with bivalves, and can be recognized by the characteristic foliated lamellar microstructure of the shell, which is composed of low-Mg calcite (Flügel, 2004) (Fig. 7A). Some brachiopods are also encrusted by siliceous sponges or

microbialites (Fig. 7A). *Amsassia*, a modular coral-like organism of possible algal affinity (Sun et al., 2014), occurs as small colonies 3–10 mm wide, and consist of tubes ~0.4 mm in diameter (Fig. 7B). *Rhabdotetradium*, a tetradiid genus and a clade of problematic affinity, is characterized by single tubes with four-fold symmetry (Steele-Petrovich, 2009) (Fig. 7C).

4. Interpretations

Bivalves most likely grew in situ, as inferred from their orientations and the relatively minor occurrences of disarticulated shells.
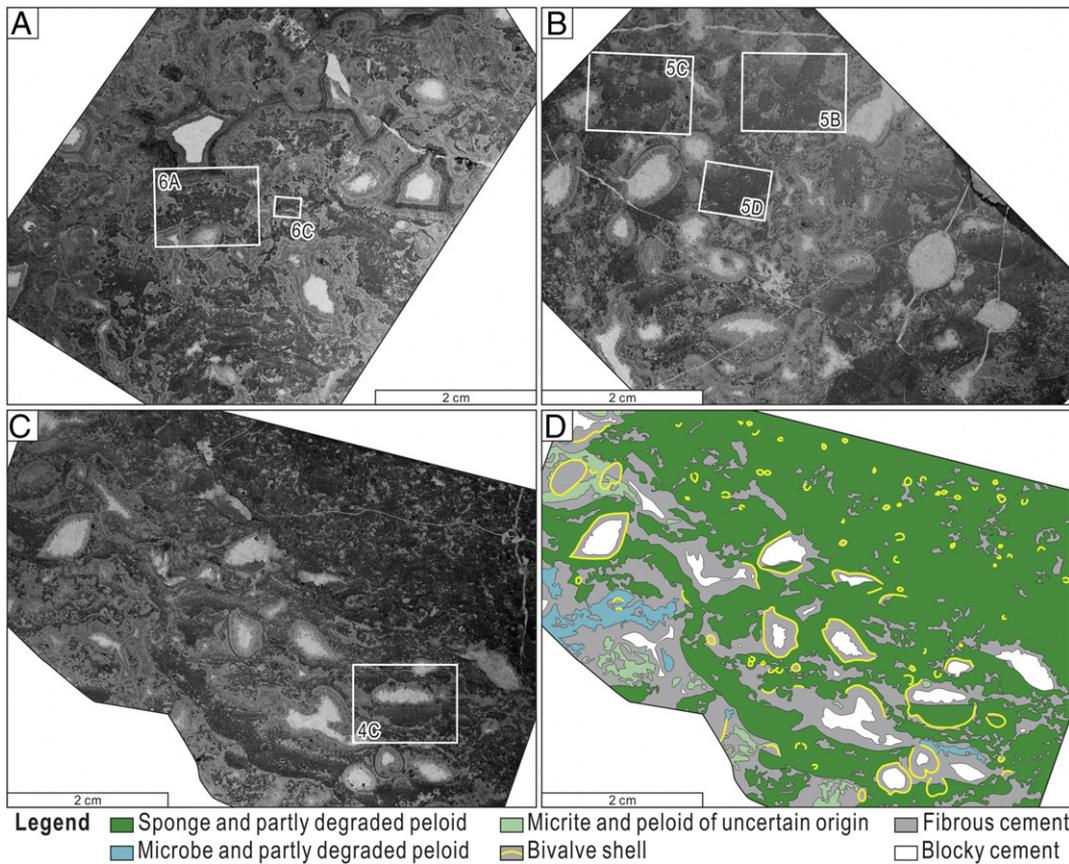
Fig. 3. Photographs of thin sections. A–C. Bivalve–siliceous sponge–microbial reef. Siliceous sponges occur mainly between the bivalves. Some sponges fill spaces within bivalves. D. Interpretive sketch of C. Note the abundant occurrences of siliceous sponges and small bivalves embedded within the sponges. The locations of images in subsequent figures are indicated by rectangles. All thin sections are oriented normal to the bedding.
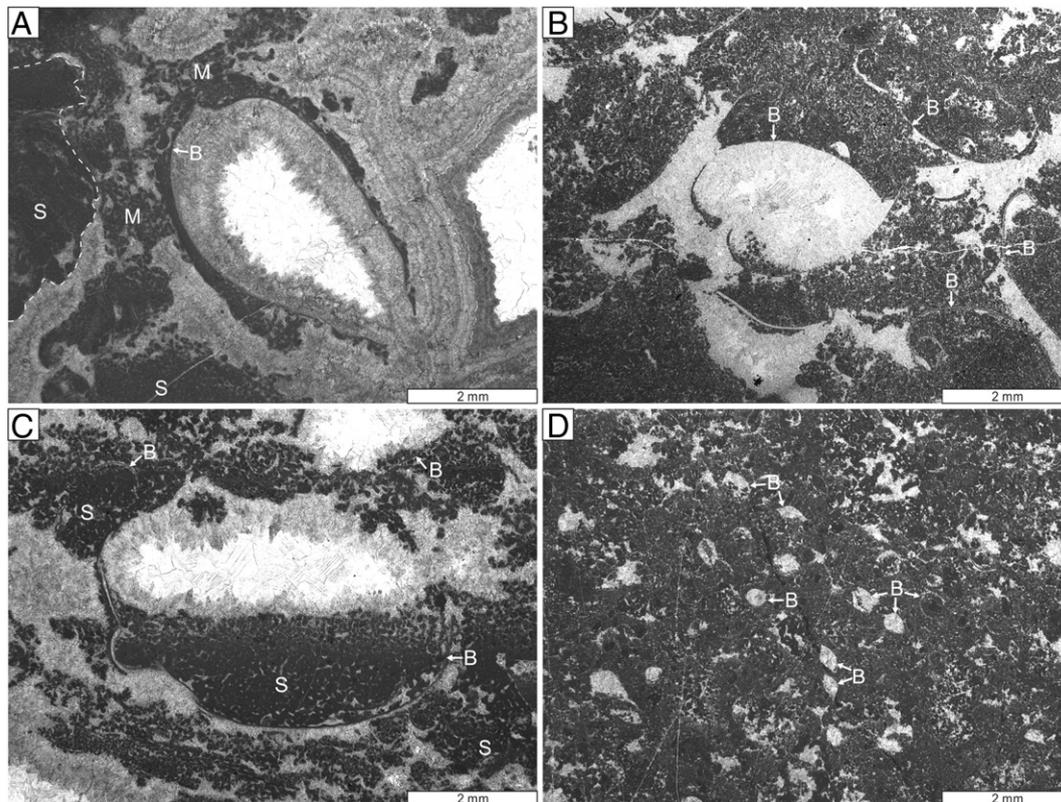
Fig. 4. Photomicrographs of bivalves. B, bivalve; S, sponge; M, microbe. A. Bivalve encrusted by thin microbial components. Note the occurrence of several growth stages of fibrous cement. B. Relict of a bivalve shell. The shell is surrounded by micrite (possibly of sponge origin) and filled with calcite cement. C. Bivalve shell containing a sponge spicule network within it, showing a geopetal structure. D. Many small bivalves occur within the partly degraded sponge spicule network.

Occurrences of siliceous sponges attached to bivalve shells indicate that the siliceous sponges encrusted the bivalves or grew within their shells, thus enlarging the reef mass (cf. Kwon et al., 2012) (Fig. 8A). Occurrences of spicules aligned with the surfaces of bivalve shells suggest that the bivalves were not borers that destroyed the original fabrics of the sponges (cf. Carter and Stanley, 2004); rather, the sponges would have grown posterior to the bivalves and attached to their shells. The irregular outer morphology of spicule networks suggests that the siliceous sponges were able to adapt to empty spaces and/or were degraded and only partially preserved during diagenesis. It has been widely suggested that sponges are degraded by anaerobic bacteria during early diagenesis, forming micrite and peloidal fabrics (Reitner, 1993; Reitner et al., 1995; Warnke, 1995; Webb, 1999; Neuweiler and Burdige, 2005; Neuweiler et al., 2007; Adachi et al., 2009). Gradational changes in sponge spicule networks to peloids would also have occurred by anaerobic bacterial degradation, resulting in the formation of micrite and stabilized spicule networks (Neuweiler et al., 2007). Bacterially produced peloids would have subsequently settled on the spicule networks, forming geopetal fabrics (Riding and Tomás, 2006). Microbes growing on pre-existing surfaces (e.g., bivalves or siliceous sponges) would have helped stabilize the underlying substrate (Fig. 8B).

The primary builders of the reefs were therefore bivalves, siliceous sponges and microbes, which were then stabilized by additional siliceous sponges and microbes. Some sponges occupied the internal spaces of bivalve shells as cryptic dwellers (Delecat et al., 2001; Hong et al., 2014; Lee et al., 2014a; Park et al., 2015; Li et al., in press). The empty spaces between biotic components were filled mainly with fibrous calcite cements that precipitated as early marine cements, which were widespread during the Ordovician greenhouse period (e.g., Pratt and James, 1982; de Freitas and Mayr, 1995; Tobin et al.,

1996) (Fig. 8C). Rapid precipitation of these cements was critical for reef formation, as they stabilized the reef framework (Webb, 1996). The remaining pore space in the reefs would have been filled by blocky cements that formed during the burial stage (Marshall and Ashton, 1980).

Co-occurrences of bivalves and siliceous sponges in these Middle Ordovician reefs suggest a symbiotic relationship between the two organisms. In modern environments, bivalves are often associated with sponges, being either covered by sponges (e.g., *Arca noae* and *Lopha cristagalli*) (Marin and Belluga, 2005) (Fig. 9) or embedded in sponges (*Vulsella* and *Crenatula*) (Tsubaki and Kato, 2012). These modern bivalve–sponge associations are commonly interpreted as mutualistic relationships. When sponges are attached to bivalve shells, the risk of predation of the bivalves is significantly reduced, while the sponges acquire suitable sites for growth (Pond, 1992; Marin and Belluga, 2005). On the other hand, when bivalves are embedded within sponges, the bivalves are protected from predators, and the sponges can utilize the bivalve shells as endoskeletons (Tsubaki and Kato, 2012). Similar mutualistic interactions between sponges and bivalves were presumably present in Chenluzhen reefs; the former example is similar to sponges encrusting large bivalves (Fig. 5A–C) and the latter resembles small bivalves embedded within sponge spicule networks (Figs. 4D and 5D). This study therefore raises the possibility that symbiotic bivalve–sponge interactions evolved as early as the Middle Ordovician.

5. Discussion: implications of the bivalve–siliceous sponge–microbial consortium for reef evolution

Skeletal-dominated reefs became widespread for the first time in the history of the Earth by the Middle Ordovician (Webby, 2002). Various
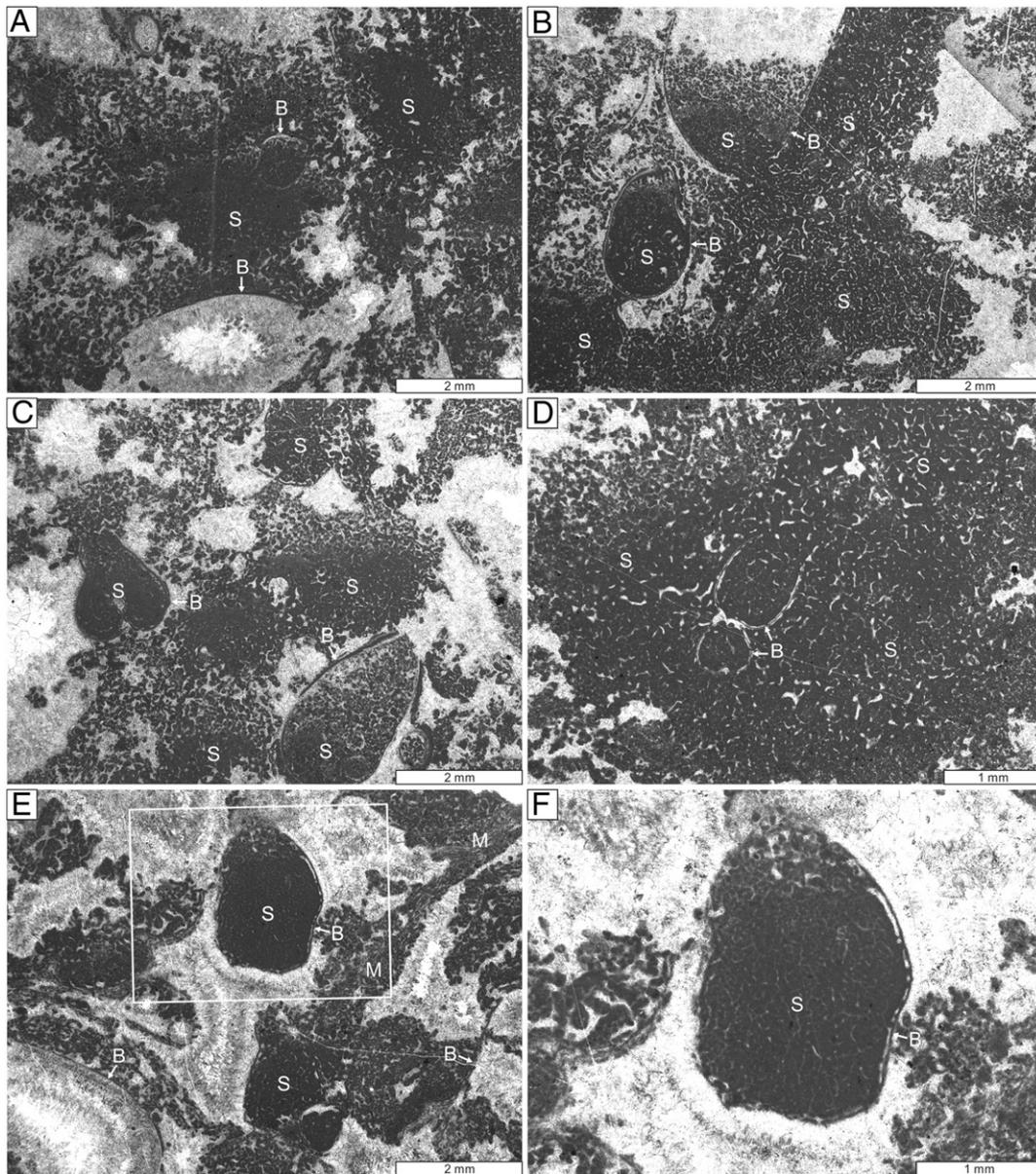
Fig. 5. Photomicrographs of siliceous sponges. B, bivalve; S, sponge; M, microbe. A. Siliceous sponge encrusting a bivalve shell. A small bivalve shell occurs within the spicule network. B. Spicule network attached to the outside of a bivalve extends to inside the bivalve shell. C. Complex relationship between sponges and bivalves. Some sponges occur within the bivalve shell, and some outside of the shell. D. Close-up of sponge spicule network. Note the occurrence of small bivalves embedded within the network and spicules aligned along the edges of the bivalve shells. E. Co-occurrence of sponge spicule networks, bivalve shells, and microbes. F. Enlargement of the area indicated by the rectangle in E, showing well-preserved spicule networks within a bivalve shell.

reef-building associations emerged during the Ordovician, some of which survived and flourished through the Middle Paleozoic, whereas others occurred for only a limited time or in restricted regions (e.g., Kwon et al., 2012; Lee et al., 2014b). The diversity of Ordovician reef-building associations reflects the advent of various organisms and their incorporation as reef-builders during the GOBE. However, to date, bivalves have not generally been considered as reef-building biota during the Ordovician (Webby, 2002), suggesting that the bivalve–siliceous sponge–microbe consortium examined in this study is unique. On the other hand, sponges are considered to have been important reef components throughout the Ordovician. For example, lithistid sponges were one of the most important reef builders during the Early Ordovician (Webby, 2002; Adachi et al., 2009). Although the importance of siliceous sponges as reef-builders decreased with the

advent of other metazoan reef-builders (e.g., stromatoporoids, corals, and bryozoans), they were still important components of Middle and Late Ordovician reefs (e.g., Desrochers and James, 1989; James and Klappa, 1989; Kwon et al., 2012). Therefore, it is necessary to discuss the nature of reef-building bivalves so as to more fully understand this unique consortium.

Reef-building bivalves that flourished in other geological periods include the Triassic–Jurassic genus *Placunopsis* (Pruss et al., 2007), Cretaceous rudists, and Mesozoic–Recent oysters (Wood, 1999; Delecat et al., 2001). These typical reef-building bivalves do not, however, exhibit the bilateral symmetry characteristic of bivalve shells. The shells of *Placunopsis* and oysters are asymmetric, and the shells of rudists are cone-shaped; thus, these taxa possess the ability to attach to irregular hard substrates, including the shells of other individuals, and are
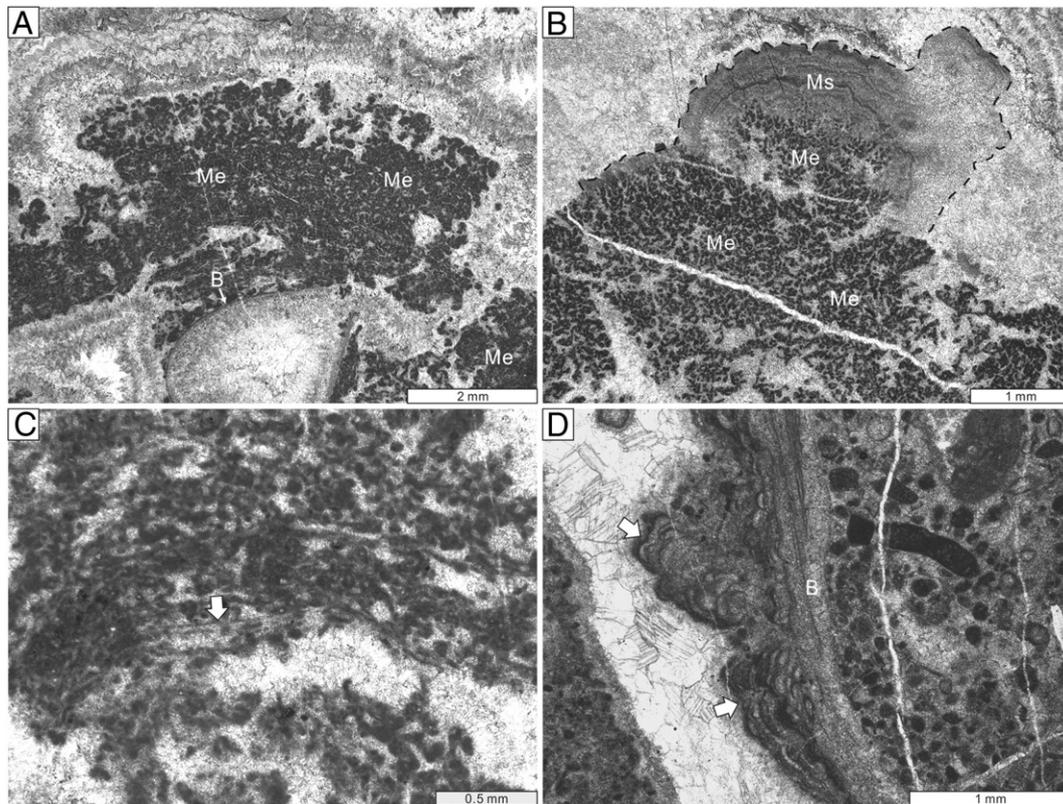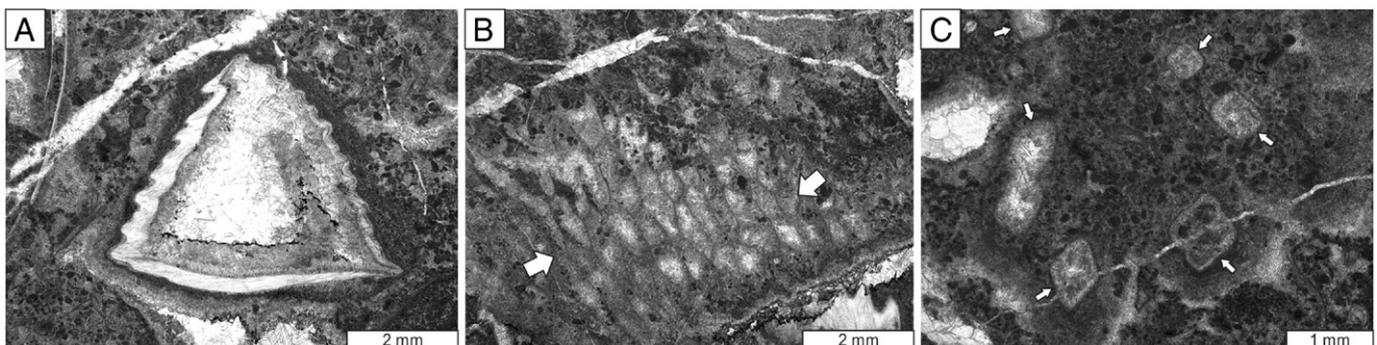
Fig. 6. Photomicrographs of microbes. B, bivalve; Me, *Epiphyton*-like microbe; Ms, microstromatolite. A. *Epiphyton*-like microbes, showing branching and bush-shaped patterns. These calcified microbes occur on top of peloids of microbial origin, which encrust the bivalve. B. Colonies of *Epiphyton*-like microbes covered by microcrystalline microstromatolite. C. *Girvanella* (arrow) embedded within peloidal fabric. D. *Renalcis*-like microbes (arrows) encrusting a bivalve shell.

hence specialized for reef-building (Pruss et al., 2007). It is not yet possible to state whether the Chenluzhen bivalves possessed a similar ability to form reefs. However, their symmetric shapes and the absence of mutually attached bivalves suggest that these bivalves were at least not as specialized as rudists or oysters for attaching to hard substrates. A recent study of an Early Triassic sponge–bivalve–microbe–serpulid reef with symmetric bivalves suggests that symmetric bivalves were also important reef constituents (Brayard et al., 2011). Sponges in this Early Triassic reef were encrusted on bivalve shells and occupied space within the bivalve shells, thus living in cryptic habitats. Although further studies are required, the current study suggests that bivalve–sponge–microbe reef-building consortia in the Phanerozoic evolved from bivalves with symmetric forms, which later evolved into non-
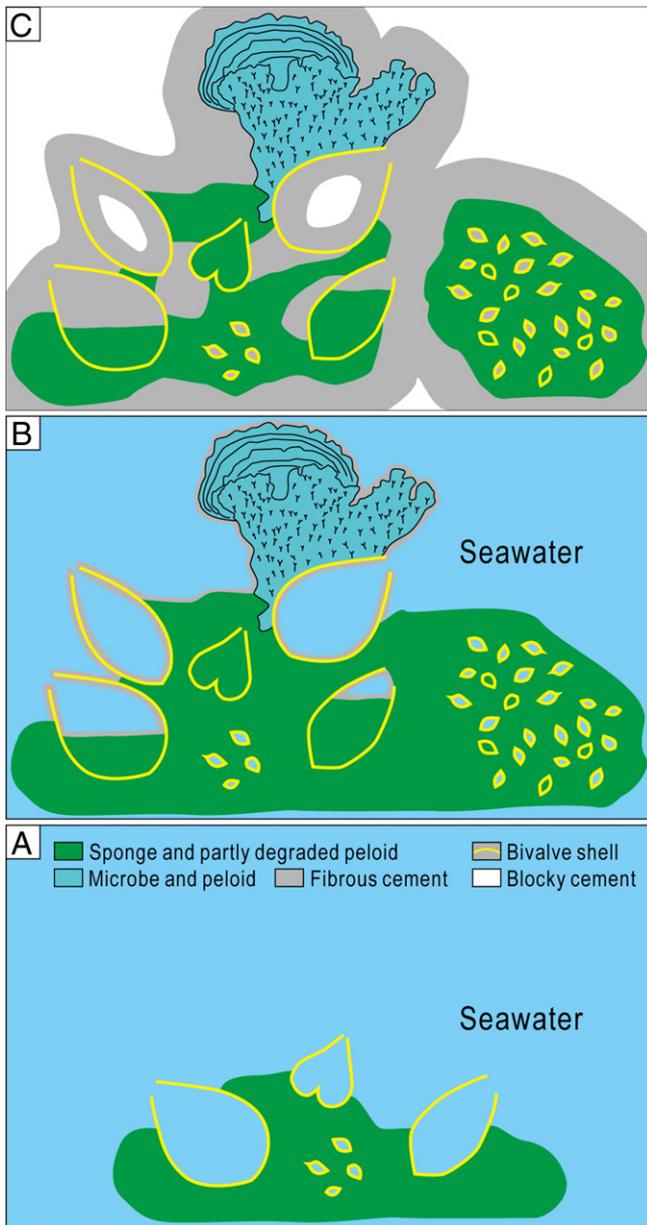
symmetric epibiotic forms specialized for attachment to hard substrates and for reef building; such forms could have existed throughout the Phanerozoic.

6. Conclusions

A bivalve–siliceous sponge–microbial reef was discovered in the western part of the North China Platform. Bivalves, siliceous sponges and microbes (calcified microbes) formed the primary reef structures, which were stabilized by encrusting siliceous sponges and microbes (calcified microbes and microstromatolites). Fibrous cements were precipitated during the early stages of reef formation, thus strengthening the reef framework. The bivalve–siliceous sponge–microbial reef

Fig. 7. Photomicrographs of minor components. A. Brachiopod encrusted by thin micritic laminae. B. Sub-longitudinal view of *Amsassia* (arrows). C. *Rhabdotetradium*, showing its characteristic four-fold symmetry (arrows).
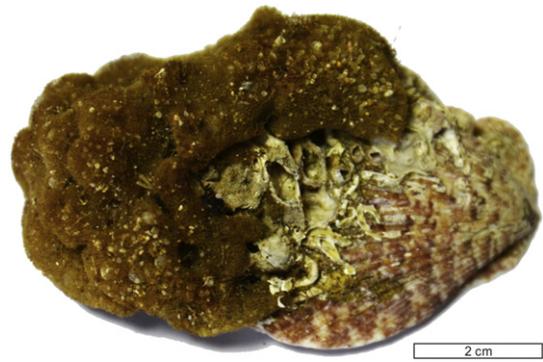
Fig. 9. Modern example of siliceous sponge encrusting a bivalve shell. Sample from the east coast of the Korean Peninsula (37°30′54″N, 129°07′34″E).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.palaeo.2016.05.034. These data include the Google map of the most important areas described in this article.

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Fig. 8. Model of the growth of bivalve–siliceous sponge–microbial boundstone. A. Large bivalves grew on sponges and were partly surrounded by them. Small bivalves dwelled within the spongocoels of sponges. B. After the death of the bivalves, the sponges filled the empty spaces within the bivalves. In some cases, microbes encrusted the sponges. C. Sponges were degraded after death, and fibrous cements were precipitated between the biotic components in situ or during early burial stages. Blocky cement was precipitated during late diagenesis.

represents a new type of Ordovician reef association, indicating symbiotic relationships among the metazoan reef-builders. Together with other associations of Ordovician reef-building organisms, this association suggests that the diversity of Ordovician reef-building communities was higher than previously thought. Such a reef-building association composed of symmetric bivalves may have evolved into an association of non-symmetric bivalves specialized for reef building during the latter part of the Phanerozoic.

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